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NOTES AND LITERATURE

BOTANY

The Origin of a Land Flora.[1]—Speculations concerning the origin of the higher plants have always had a special attraction for the botanical student whose work extends beyond the limits of mere collecting and tabulation. Perhaps the very fact that we can never expect to discover all of the factors concerned with the evolution of the vegetable kingdom, and that our conclusions are always liable to be materially altered through the discovery of new facts, or a different interpretation of those already known, gives an added zest to the hunt for new forms or the discovery of new facts about those already known which may add another stone to the edifice which is being slowly built up.

The volume under consideration is one deserving more than passing attention from the student of plant evolution. Not only is it the work of one of the keenest investigators of some of the most difficult problems with which the botanist has to deal, but the book represents the fruits of many years' arduous labor, but evidently a labor of love, which has yielded results of the utmost importance and provides a mine of accurate information, presented in an unusually clear and attractive style. From a literary standpoint, it might well be recommended as a model to some of our scientific writers who, it must be confessed, do not always compare very favorably with their English colleagues in the matter of literary form.

Aside from the wealth of facts brought together in this handsome volume, illustrated by many admirable illustrations, the reader constantly encounters speculations, sometimes almost startling in their originality, with which he may not always agree, but which are certain to set him thinking deeply; and we believe that this book will be a great stimulus to the further exploration of many obscure, but very important, questions bearing upon the affinities of the higher plants.

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[1] The Origin of a Land Flora: A Theory based upon the Facts of Alternation. By F. O. Bower, ScD., F.R.S., Regius Professor of Botany in the University of Glasgow. Pp. xi + 727, many illustrations. New York, The Macmillan Co.; London, Macmillan and Co., Limited. $5.50 net.

It is not necessary to remind botanists of the high standing of Professor Bower's numerous contributions to science. Not only has such work as his great monographs on spore-producing organs put him in the first rank of morphologists, but his interpretation of the facts of comparative morphology, and his more speculative papers on alternation of generations and the origin of the land plants, have strongly influenced all recent theories on these important questions. Professor Bower is thus peculiarly fitted to treat this difficult subject, and it is with special gratitude to the author that botanists will welcome this admirable presentation of the results of his many years' labors.

It is generally admitted that the existing land flora, *i. e.*, the Archegoniatæ and seed plants, are the descendants of some fresh-water plants probably allied to certain green algæ; but the way in which these typically aquatic organisms gave rise to forms markedly terrestrial in habit is one of the questions about which there are very diverse opinions. Professor Bower has long contended, and we believe that he has overwhelming evidence on his side, that the characteristically terrestrial modern plant type, *i. e.*, the sporophyte or neutral generation of the ferns and seed plants, is the product of the evolution of the zygote or resting-spore of some fresh-water algal type, the result of the union of the sexual cells, or gametes, and in most cases is an adaptation to surviving periods of drought to which these plants are liable. That is, the sporophyte is from its inception a terrestrial or subaerial phase interpolated between the active aquatic growth periods. This is the "antithetic" theory of alternation, and it is this thesis, opposed to the "homologous" alternation which of late has been defended by a number of eminent botanists both at home and abroad, that Professor Bower defends in the present volume.

In his previous work, Professor Bower has elaborated his theory of the important part that the sterilization of potentially sporogenous tissue has played in the evolution of the sporophyte of the higher plants. Particularly has he made this clear in his important series of monographs on the development of the spore-producing organs of the Pteridophytes. The present volume is divided into three parts: (1) The Statement of the Working Hypothesis, (2) Detailed Statement of Facts, (3) Conclusion.

It has been rather the fashion of late to belittle the importance of comparative morphology, as it is evident that the plant organism, with its potentially unlimited power of regeneration and growth, is extremely plastic and responds promptly to any external stimuli. Nevertheless, the facts of comparative morphology are too evident to be ignored, and although the modern student must carefully check his work by the data furnished from experimental morphology, physiology, and paleontology, it still is evident that the surest clues to relationship must be sought in a comparison of corresponding structures and the facts of ontogeny.

The phenomena of alternation of generations as exhibited by the higher plants are familiar to the botanist. The plant shows two marked life phases, first the sexual phase, or gametophyte, and second the neutral generation, arising from fertilization, the sporophyte. In all but the highest plants, the seed plants, the gametophyte betrays more or less clearly its aquatic origin. It is usually poorly adapted to resist dryness. Water is necessary for fertilization, as the male gametes are ciliated and the mature sexual organs require water for their proper dehiscence. In the lower types, like the simple liverworts, the gametophyte is relatively larger and plays a much more important rôle in the plant life than does the insignificant sporophyte, which is short-lived and dies as soon as it has shed its spores, whose production is the aim of its existence. The sporophyte in the lower forms is never an aquatic structure, but receives its water indirectly from the gametophyte with which it is permanently in intimate association.

With the increasing specialization of the Archegoniates, several lines of development were inaugurated showing several different types of specialization both in the gametophyte and in the sporophyte. The gametophyte reaches its culmination in the higher mosses which seem to show the limit of the possibility of adapting the essentially aquatic gametophyte to life on land. The further development of the land plants is therefore bound up with the elaboration of the terrestrial phase of the plant's life history, *i. e.*, the sporophyte. With the increasing importance of the latter there is a progressive reduction of the gametophyte which culminates among the Pteridophytes in the extremely reduced gametophytes of the heterosporous forms like Marsilia or Selaginella.

It is not likely that any existing liverworts represent very nearly the direct ancestors of the Pteridophytes or ''Vascular

Cryptogams." It may be said, however, that some remarkable parallelisms, if not real homologies, are shown by the peculiar Anthocerotes, and there is a progressive development of the sporophyte in both liverworts and true mosses which hints at least at the course of evolution which finally resulted in the entirely independent sporophyte of the ferns. The evolution of the sporophyte consists in a constantly increasing development of sterile or non-sporogenous tissues, which assume the character of green assimilative tissue, etc., and it may finally develop definite external organs, roots and leaves, the former connecting the sporophyte with the earth and making it quite independent of the gametophyte. Finally, spores are produced, always in a perfectly uniform manner in groups of four, and the life history is complete.

While only a relatively small number of forms have been investigated, it is pretty certain that the sporophytic tissues normally have nuclei with twice the chromosome number found in the cells of the gametophyte, this being the result of the doubling of the chromosomes due to the fusion of the gametes. The reduction of the chromosomes occurs in the tetrad division resulting in the spores, which therefore possess the normal gametophyte number.

The formation of the sporophyte by apogamy or direct budding from the prothallium, and the various buddings of the gametophyte from the leaves of the sporophyte, are the strongest arguments in favor of "homologous" alternation; but the facts of apogamy and apospory may be explained as cases of adventitious budding analogous to so many cases found in the seed plants, and much more evidence is needed to show that they are normal rather than pathological.

Comparing the sporophytes of the Bryophytes and Pteridophytes, the latter are distinguished by the development of external organs. A more or less conspicuous central axis has appendicular organs, leaves, roots and sporangia, the latter being the characteristic organs which distinguish the different types of vascular plants. They may be supposed to have arisen from the more or less complete segregation of masses of sporogenous tissue from the originally continuous layer of some such form as Anthoceros. The gradual evolution of the sporangium from the large indefinite sporocysts like those of Ophioglossum to the very definite sporangia of the highly specialized leptosporangiate ferns can be clearly followed in existing types. Professor Bower does not regard the Ophioglossales as related to the true ferns, but from this view we feel obliged to dissent.

As might be expected, much stress is laid upon the "Theory of the strobilus" with which Bower's name is especially associated. This theory assumes that from some bryophytic sporangium, perhaps not very different from that of Anthoceros, by the segregation of definite sporangia each subtended by a leaf-like organ originating from the sterile tissue between the sporangia, a cone or strobilus would be derived, *i. e.*, an axis upon which are borne a number of leaves usually spirally arranged, each one subtending a sporangium. This condition is still met with in some of the simple species of Lycopodium like *L. selago* and it is an extremely ancient one.

This theory of the strobilus when applied to the Lycopods has very much in its favor, and is certainly the most plausible explanation yet put forward as to the origin of the Lycopods; but is not so convincing when one tries to reduce the ferns also to the strobiloid type. It is true that in the Cycads, which are doubtless of fern affinity, a strobilus is present, but there is very strong reason to suppose that it is a secondary condition.

The chapter on "Embryology and the Theory of Recapitulation" is a very sane treatment of an extremely difficult problem. While recognizing that the first students of vegetable morphology went much too far in their insistence upon the importance of the exact succession of cell divisions in the young embryo in their relation to the subsequent organs of the plant, nevertheless it is unquestionable that the early divisions of the embryo are to a certain extent a recapitulation of the early phylogeny. It must be remembered that the young embryo has been subjected for countless ages to practically the same conditions, and that under these conditions certain definite early segmentations should be fixed is merely what would be expected. One of these conditions is the action of gravity and this beyond question is the most important factor in determining the marked polarity of the embryo. As to the general application of the theory of recapitulation to the later stages of development, as Professor Bower very well points out, great caution has to be used, but nevertheless within proper limits it is justified.

Professor Bower maintains that there is but one type of leaf.

All leaves, he thinks, are primarily sporophylls. Foliage leaves are reduced sporophylls and cotyledons, and "protophylls" mere modifications of the foliage leaves. This is not, however, a view that can be accepted without some qualification. While undoubtedly on the theory of antithetic alternation, spore-bearing structures must have preceded foliage leaves, it may be questioned whether these primary spore-bearing structures at least in the case of the Ophioglossaceæ and Equisetaceæ, were not rather of the nature of sporangiophores than sporophylls in the strict sense of the word. If such is the case, the sterile leaves would be outgrowths of the sporangiophores, or even independent structures rather than direct metamorphoses of sporophylls.

From a study of the anatomical evidence, the conclusion is reached that the primitive state in the Pteridophytes was one in which the axis was structurally dominant in the shoot, and the type of cauline bundle a solid monostele. It is also concluded that the bipolar, radially symmetrical condition of the sporophyte is more ancient than the dosi-ventral condition.

The problem of the origin of the roots of the vascular plants by means of which the independence of the sphorophyte is finally secured is recognized as a very difficult one. In some Lycopods no root is formed in the embryo until after several leaves have been developed, and the name "protocorm" has been proposed for this early undifferentiated plant-body, the assumption being made that it represents an ancient condition antedating a plant-body with true leaves. Professor Bower, however, is inclined to doubt the accuracy of this hypothesis.

While recognizing the great value of the evidence of paleophytology, and the important contribution that the study of fossils has made to our knowledge of the evolutionary history of the Pteridophytes it is pointed out how very little light has been thrown by this science upon such fundamental questions as the origin of the bryophytic sporogonium or that of the leafy sporophyte.

In chapter nineteen are discussed the difficulties of determining whether amplification or reduction has been the more important factor in determining the course of evolution in certain cases. Chapter twenty contains a succinct summary of the Working Hypothesis and concludes Part I.

Over 400 pages of text with many admirable illustrations are devoted to Part II, "A Detailed Statement of Facts." This is an excellent account of the sporophytic structures of the Archegoniates and would by itself form an important volume. As might be expected in a treatise on land plants, and from the author's previous works, the Pteridophytes are the principal subjects of study, only two chapters out of twenty being devoted to the Bryophytes. Space forbids even an outline of the great mass of facts brought together, not the least interesting and important being those derived from a study of the fossil forms which of late have attracted so much attention. Very little space is given to the study of the gametophyte, and while no doubt in the problem of the origin of a land-flora the sporophyte is much the more important factor, still we can not but feel that in some cases, a careful study of the gametophyte would have resulted in some different conclusions and would have served as a useful check. Thus all the recent work on the gametophyte of the Ophioglossaceæ emphasizes the strong similarity in the reproductive organs of these forms and those of the Marattiaceæ and makes more probable than ever a real relationship existing between these two orders of eusporangiate ferns.

There are recognized three phyla or main developmental series of Pteridophytes, the Lycopods, the "Sporangiophoric Pteridophytes" and the ferns, excluding from the latter the Ophioglossaceæ which Professor Bower thinks at present had best be treated as a fourth phylum, although he concludes that there is good evidence of a more or less evident affinity with the "Sporangiophoric Pteridophytes."

The isolated position of the Lycopods is recognized by Professor Bower, and there certainly is very strong reason, both from a study of the gametophyte and sporophyte, for assigning to this group an origin quite apart from that of the other Pteridophytes.

The most radical departure from the ordinarily accepted arrangement of the Pteridophytes is the establishment of the group of "Sporangiophoric Pteridophytes" which includes the Equisetales and the fossil Sphenophyllales with which latter group are included the anomalous Psilotales, which have usually been associated with the Lycopods, but whose isolated position has for some time been clearly recognized. To the sporangiophoric Pteridophytes Bower also thinks the Ophioglossales may be related. The sporangiophore is defined as a more or less elongated vascular stalk upon which sporangia are borne. The sporangiophores are considered to be organs *sui generis* not a modification of either a foliar or cauline organ. The question is left open whether the sporangiophore is to be regarded as the elaboration of a single sporangium, like that of Lycopodium, but it seems to us that the origin of the sporangiophore as a compound structure from the beginning, is more in harmony with the facts of comparative anatomy.

The acceptance of this view will we believe help to solve some of the most puzzling questions as to the affinity of the primary pteridophytic stocks. While convinced of the real affinity between the Ophioglossaceæ and the true ferns, we have also more than once called attention to the marked resemblance between the gametophyte of Equisetum and that of the lower ferns; and it may be added that there are also correspondences in the embryo that are probably not without significance. If then we admit that the sporangiophoric Pteridophytes really represent a natural division of the Pteridophytes, it is quite conceivable that from some common ancestral form having a large green gametophyte like that of the lower ferns, two types of sporangiophoric sporophytes may have arisen, one developing the strobiloid group of sporangiophores, as in Equisetum, the other a single large sporangiophore like that of Ophioglossum. There is very good reason to suppose that the sporangiophore of the Ophioglossaceæ is not an appendage of the so-called sporophyll, but is a quite independent organ, the sterile lamina being rather an appendage of the sporangiophore than the reverse.

In spite of Professor Bower's argument we can not but feel that the resemblances between the Ophioglossaceæ and the true ferns are too numerous and exact to be explained on any other ground than that of a real affinity; but this does not lessen the importance of his explanation of their probable affinity with the Equisetales and Sphenophyllales.

The classification of the Filicales excluding Ophioglossaceæ is that already elaborated in his memoirs on spore-producing members. Three groups of the Filicales are recognized. One, Simplices, in which all of the sporangia of a sorus are formed simultaneously. Two, Gradatæ in which there is a definite success in time and space; and Three, the Mixtæ in which there is a succession in time but not in space. Six families are included in the first group. The Botryopterideæ (fossil), the Marattiaceæ, Osmundaceæ, Schizæaceæ (Marsiliaceæ)? Gleicheniaceæ and Matonineæ. The Gradatæ include five families. Loxsomaceæ, Hymenophyllaceæ, most Dicksonieæ, Dennstædtiinæ, Cyatheaceæ (Salviniaceæ)? The remaining families often grouped together as Polypodiaceæ form the group of the Mixtæ.

The Botryopterideæ comprise some of the earliest known fossil Filicales. Their affinities, however, are somewhat obscure, and the group seems to have been a synthetic one. They show certain evidences of affinity with the Marattiaceæ also with the Osmundaceæ and Hymenophyllaceæ. It might also be suggested that a comparison of the sporangium might be made with Botrychium and perhaps Helminthostachys.

We must pass over with brief mention the very detailed account of the ferns which occupies over 150 pages of the text. The tendency in the evolution of the sporangium is very clearly from the larger eusporangiate type of the Marattiaceæ reaching its maximum in Kaulfussia, where nearly 8,000 spores occur in the single sporangium, to the numerous, small leptosporangiate sporangia of the Mixtæ where there may be only from 8 to 64 spores. It may be added that the sporangia of Ophioglossum represent a still more primitive type, both in their large size, their indefinite limits and very great number of spores.

The assumed relation of the different families of the Filicales is graphically shown in the diagram on page 653.

Part III is a summary covering some sixty pages. The most important conclusion may be briefly stated as follows: "*Certain Algæ suggest in their post-sexual phase how the initiation of a sporophyte may have occurred, but there is no sufficient reason to hold them as being in the actual line of descent of archegoniate forms.*" "*Both Mosses and Liverworts may with probability be held to be blind branches of descent,* which illustrate nevertheless phyletic progressions that illuminate the origin of sterile tissues from those potentially fertile, and the establishment of a self-nourishing system in the sporophyte." "*It may accordingly be concluded as probable that the prothallus of early Pteridophytes at large was a relatively massive green structure, with deeply sunk sexual organs.*"

The Lycopodiales stand by themselves in the simplicity of the sporangial arrangement and constitute a type of extreme antiquity, which has come down practically unaltered to the present day. Their comparative study may be conducted independently of other phyla: for there is no reason to think that they were derived from any other known vascular type. . . . *The condi-*

tion actually seen in the 'Selago' type may be held as truly primitive, and Lycopodium Selago, *with its imperfectly differentiated shoot, is in fact a near approach in a living species to the ideal primitive form which emerges from wide comparative study of the phylum as a whole.*''

''*The functionally identical parts designated sporangiophores and sporangia are cognate parts; it appears probable that the sporangiophore is itself a consequence of elaboration of a simpler type of spore-producing member, of which the sporangium of* Lycopodium *is an example, while the trabeculæ in* Isoetes *and* Lepidostrobus Brownii *suggest a mode of origin of the septate state. If this were so, then the sporangiophore would have been distinct in its phyletic origin from the bract-leaves, which habitually subtend the spore-producing members, whether they be sporangia or sporangiophores.*''

''*The phyletic relationship of the Sphenophyllales and Equisetales has undoubtedly been a very close one; the distinguishing features are not to be found in the primary plan or construction of the shoot, so much as in the secondary modifications of number and relation of the appendages, and of their branching, together with changes in the originally protostelic structure of the axis. Such considerations support the conclusion that the Sporangiophoric Pteridophytes constitute a brush of naturally related phyletic lines.*''

The Ophioglossales are regarded as an ascending series of forms the ''*spike illustrating various steps in the increasing complexity of a body of the nature of the sporangiophore.*'' ''The whole unbranched shoot is a single strobilus bearing leaves of which all are potentially fertile and the majority actually so.'' ''*The Ophioglossaceæ appear to have been an upgrade sequence, sprung from some sporangiophore stock, and bearing no near relation to the large-leaved ferns.*''

''*The Filicales were ultimately of strobiloid origin, but have undergone amplification of their leaves analogous to, but phyletically quite distinct from what is seen in other Pteridophytes, and carried to a higher degree.*''

''One chief reason for regarding the lines of the Filicales and Ophioglossales as distinct lies in the difference of position of the spore-producing members. It has been argued above (p. 633) that the soral condition was primitive for ferns, and that *the sorus is a body similar in kind to the sporangiophore, the two* *being alike in function, in structure, and in capacity for fission and extension: the number and position are points of difference.*"

The Filicales are considered to be a phylum showing fundamentally the strobiloid characters, but secondarily modified in relation to their pronounced megaphyllous habit. "*Accordingly, the Filicales appear as the most divergent phylum of homosporous Pteridophytes.*"

"*Comparison of the several phyla, as represented both by their fossil and their modern representatives, leads in each case towards the recognition of a primitive type, and its construction in the several phyla has certain features in common.* The chief of these are the definition of axial polarity in the first initiation of the embryo: the continued apical growth; the radial construction of the shoot: the origin of the appendages laterally from the axis by enation, and in strictly acropetal order: a protostelic structure of the conducting system of the axis, and a leaf-trace composed of a single strand."

"The sporophyte . . . probably arose originally as a structure of limited size, and unbranched, upon a prothallus of considerable dimensions, and producing *Homosporous Spores.*"

"The adoption of *Heterospory*, and of the *Seed Habit* supervened later. This, while it has led to the final independence of the land flora as regards external fluid water for the completion of its life-cycle, has brought as a secondary consequence a widespread reduction."

"The final goal of all organic development is the establishment of new individuals. The evolutionary story of the sporophyte illustrates this in two distinct ways. *In the prior and non-specialized homosporous forms large numbers of germs are produced: . . . consequently amplification of the whole sporophyte is the leading characteristic of these earlier types; . . . In the later and more specialized heterosporous forms and particularly in the Seed Plants with their more refined methods, individual precision supersedes mere numbers; and reduction of the propagative system has been its usual concomitant.*"

"The sporophyte, which is the essential feature in the Flora of the Land, is referable back in its origin to post-sexual complications: *it appears to have originated as a phase interpolated between the events of chromosome-doubling and chromosome-reduction in the primitive life-cycle of plants of aquatic habit.*"

DOUGLAS HOUGHTON CAMPBELL.